

POLLINATION AND VARIATION IN THE SUBTRIBE
CATASETINAE (ORCHIDACEAE)

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ABSTRACT

The natural history of the subtribe *Catasetinae* is briefly discussed. The present taxonomic status of the genera *Catasetum*, *Cycnoches* and *Mormodes* is reviewed, and the phylogenetic relationships between the genera and the species groups in *Catasetum* are discussed. The production of separate male and female inflorescences is explained as being triggered by the relative amounts of sunlight received by the plants. Those plants which receive filtered sunlight produce male flowers and those receiving full sunlight produce female flowers. The pollen throwing apparatus and the pollination mechanisms of the various genera are discussed on the basis of field observations. Variation in populations of *Catasetum platyglossum* Schltr. and *C. macroglossum* Rehb. f., which are sympatric on one margin of their ranges in western Ecuador, is evaluated. The two populations were once separated by a band of rainforest on a low mountain range. This region has become sufficiently arid for the species to come together and pollination by a common agent has produced several highly variable hybrid swarms. CALAWAY H. DODSON, Missouri Botanical Garden, 2315 Tower Grove Ave., St. Louis 10, Missouri.

INTRODUCTION

This paper has been written to discuss in a general manner, the pollination, pollination mechanisms, taxonomy, relationships among the members, sexuality and population variation of the *Catasetinae*. It is hoped that in this manner a basic reference will be formed for forthcoming papers dealing with specific phenomena in the group. The present status of taxonomy in the group is deplorably bad and classic herbarium techniques of study are of little or no help in critical groups, due to the general paucity of specimens and the destruction of important characters in their preparation. Field studies of population variation will surely be important in clarifying the taxonomy of the group.

The subtribe *Catasetinae* has been of interest to both botanists and horticulturists since the members of this group became known. The complicated mechanisms enabling forcible discharge of the pollen apparatus found in most species have been described and commented upon by various authors. Such highly evolved mechanisms capture the interest of anyone from the orchid enthusiast to the evolutionist and considerable literature is available on the mechanics of these systems. However, very few accurate observations have been made upon the natural pollination of these plants in the field. Authoritative accounts have been published of pollination in *Cycnoches* by Allen (1952) and in *Catasetum* by Darwin (1872), based on observations by Crüger. Unfortunately, Crüger's account was based on very superficial observation and both papers contain some errors and omit considerable pertinent information.

This group is unique among the *Orchidaceae* for having members which produce separate staminate and pistillate flowers. They are also unique in having the capacity of forcibly flinging the pollinarium at an insect pollinator. The pollinarium is thereby fixed in such a position on the insect that it may easily complete the pollination phase of the life cycle by delivering the pollen to the stigma of another flower.

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TAXONOMY OF THE GROUP

As presently constituted the subtribe *Catasetinae* consists of three genera, *Catasetum* Rich. with approximately 70 nominal species, *Mormodes* Lindl. with about 40 nominal species and *Cynoches* Lindl. with seven species. The group is limited to the New World tropics where its members occasionally form a conspicuous element in the orchid flora. Its closest affinities probably lie with *Cyrtopodium* R. Br. and *Galeandra* Lindl. of the subtribe *Cyrtopodiinae*. While the linking members between these genera and the *Catasetinae* are now extinct, the gap is not great.

Catasetum has been divided into two subgenera; *Clowesia* and *Catasetum*. The subgenus *Clowesia*, as treated by Mansfeld (1932) and Hoehne (1942), consisted of eight species all of which produce bisexual flowers and have no antennae on the column to trigger the expulsion of the pollinaria. Two quite dissimilar groups have been placed together in *Clowesia* and it is my opinion that they should eventually be separated. *Catasetum roseum* Rchb. f., *C. warczewitzii* Lindl. & Paxt., *C. glaucoglossum* Rchb. f. *C. thylaciochilum* Lem. and *C. russellianum* Hook., have the lip relatively thin in substance, not adnate to the column and usually fimbriate. In *C. glaucoglossum* and *C. russellianum* the anther is only slightly sensitive and the viscidium springs down only slightly when released. These species have many characters in common with certain species of *Galeandra*. The other group consists of *C. dilectum* Rchb. f., *C. eburneum* Rolfe and *C. suave* Ames and Schweinfurth. Unfortunately, there appear to be only two species in this group, but there are three names; two of which are of uncertain application. One species, corresponding to *C. suave* of Ames and Schweinfurth (the type of this species, at the Smithsonian Institution, has been examined) occurs from Costa Rica to Ecuador. The other species is only to be found in Costa Rica and Panama. Both species are somewhat variable and the type descriptions are not satisfactory to differentiate between the two kinds of plants. These species have the lip entire, fleshy and adnate to the thick, swollen column. I feel that this group is adequately distinct from the other group of species in *Clowesia* and should be recognized as a valid genus.

The subgenus *Catasetum* as treated by Mansfeld and Hoehne consists of nearly 60 species, all producing separate male and female flowers. The subgenera *Clowesia* and *Catasetum* are not far separated in terms of evolution and the development of unisexual flowers from the bisexual group is easily traced. The column of most species of the subgenus *Catasetum* has long projections or antennae extending from each side of the anther to the center or cavity of the lip. These antennae, when touched, release the tightly stretched stipe of the pollinarium so that the viscidium is flung out and onto the thorax of the insect. Mansfeld divided the subgenus *Catasetum* into two groups; *Pseudocatasetum* and *Meizocatasetum*, the former having male flowers which are devoid of antennae and the latter having antennae. He then went further to divide *Meizocatasetum* into two groups; *Isoceras* and *Anisoceras*, depending on whether the antennae were parallel or one was bent back under the other. I have found this division to be unworkable on many occasions

in which some flowers had the antennae parallel, while others on the same inflorescence had one bent. In other instances one inflorescence would have flowers with antennae bent and another inflorescence of the same plant would have flowers with parallel antennae. The flower morphology is not particularly distinct between the two subgenera and the more advanced members of *Clowesia* closely approach the species which lack antennae in the subgenus *Catasetum*. Even in the more advanced members of the subgenus *Catasetum* hermaphroditic flowers are occasionally produced which are quite reminiscent of some members of *Clowesia*.

Cycnoches has been revised recently by Allen (1952). Allen's treatment of this genus is unusual in modern taxonomic work on the tropical Orchidaceae in that it is based on personal knowledge of the plants as living populations in the field. *Cycnoches* is composed of two distinct subgenera. In the subgenus *Cycnoches* the male and female flowers are essentially the same in form with the only significant difference being that the column is shorter and thicker with the stigma functional in the female flowers while the column is long and slender with only the anther present in the male flowers. Allen lists four species in this subgenus. The subgenus *Heteranthae* produces male and female flowers which are strikingly different. The female flowers are morphologically similar to the female flowers of the subgenus *Cycnoches* but are smaller. The male flowers are much smaller than the female flowers, are produced in considerable quantity on long pendant racemes, have a flexible claw on the lip and usually have a toothed fleshy callus. Allen lists three species in this subgenus.

Mormodes has never been revised. This is probably due to the formidable variation encountered within the populations. In several cases, characters which were previously used to separate species have been found to vary widely on one inflorescence. Certainly many of the 40 nominal species will be found not to be valid when a careful study is made of the genus.

PHYLOGENETIC RELATIONSHIPS WITHIN THE CATASETINAE

The ancestral types linking the subtribe Catasetinae with its closest allies in the Cyrtopodiinae are now extinct but sufficient correlation between the two subtribes remains to indicate relationship.

A phyletic series can be observed from *Catasetum glaucoglossum* and *C. thylaciochilum* as the simplest types through *C. russellianum* to *C. roseum* and *C. warczewitzii* in the subgenus *Clowesia*. The sensitive anther which is characteristic of the Catasetinae is not highly developed in some of the members of this group. *Catasetum discolor* of the subgenus *Catasetum* is morphologically quite similar to *C. warczewitzii* except that separate male and female flowers are produced. More advanced species are then encountered with unisexual flowers and are furnished with complicated antennae for triggering pollinia expulsion. In the latter group the species with rather similar hooded male and female flowers are probably less advanced than the species with open male flowers (such as *C. barbatum* Lindl.) which have highly developed fringes and papillae on the lip of the male flower.

The basic separation between the types of flowers produced by the major groups

of *Catasetum* is morphological but is founded upon different pollination mechanisms. In the portion of the subgenus *Clowesia* which produce less fleshy flowers the column is of necessity placed relatively near the lip in order for the pollinator to brush the anther with its upper thorax and receive the pollinarium. *Catasetum roseum*, *C. thylaciochilum*, *C. warczewitzii*, *C. russellianum* and *C. glaucoglossum* all appear to be of this type. *Catasetum dilectum*, *C. eburneum* and *C. suave* appear to be based on another system in which the bee approaches the flower, lands on the front of the open flower with its head toward the apex of the lip and its abdomen over the column, touches the triggering mechanism and receives the pollinia on the ventral side of the thorax either in front of or among the legs. In the more advanced species of *Catasetum* the bee lands upon the lip and while approaching the source of the fragrance, located in a depression or within a saccate hood, inadvertently touches one of the antennae, releasing the pollinarium which is flung for some distance to strike the pollinator. The pollinator is usually positioned in such a manner that the viscidium is attached to the upper thorax.

Cycnoches may have developed from the fleshy flowered group of species in the subgenus *Clowesia* of *Catasetum*. Though the general features of the labellum are not entirely similar in the two groups, the apparatus for expulsion of the pollinarium is very similar. Both types of flowers are designed for placement of the pollinarium on the ventral surface of the pollinator. In *Catasetum suave*, for example, the column is short and fleshy with the anther positioned on the apex of the column. The simple extension of the anther on a long, slender column would result in the same type of apparatus as found in *Cycnoches*. The triggering mechanisms for expulsion of the pollinia in the two groups are based upon leverage and tension released by lifting the apex of the anther. These two groups are the only members of the Catasetinae which use this system for propulsion of the pollinia (fig. 1). The fleshy members of *Clowesia* are normally quite uncommon in nature, perhaps an indication that they are not particularly successful. They are only found in the tropical cloud forest regions of Central and South America. These cloud forests seem to be particularly hospitable for relict and marginal epiphytic species.

Cycnoches has apparently left the bisexual flowered condition and normally only exhibits unisexual flowers. The occasional production of hermaphroditic flowers indicates that the capacity for production of bisexual flowers is not completely lost.

The genus *Mormodes* is apparently in the process of developing unisexual flowers at present. There have been reports of the production of unisexual flowers in certain species of *Mormodes* and I have encountered the same condition in a species in Ecuador. This genus is perhaps not as highly successful as *Catasetum* or *Cycnoches*. Within their range they are usually not encountered in such great quantity as the other two genera and are often quite rare. The plants are not as tolerant of adverse ecological conditions as are the related genera.

SEXUALITY

The production of unisexual flowers in these orchids has been the subject of considerable comment and discussion. It is, of course, unique in a family nearly typified by bisexual flowers. This development of polygamo-dioecious flowers appears to be in a stage of transition in certain species within the *Catasetinae*. The species within the subgenus *Clowesia* of *Catasetum* apparently produce bisexual flowers only, while the members of the subgenus *Catasetum* ordinarily produce unisexual flowers. Species of the subgenus *Catasetum* do occasionally produce bisexual flowers, and both male and female flowers are sometimes found on the same inflorescence. Within the genus *Cycnoches* no species occur which produce bisexual flowers exclusively, but bisexual flowers are found on these plants on rare occasions. Recent evidence (Allen 1959) indicates that two types of flowers are found in *Mormodes lineatum* Batem.; staminate flowers, which apparently function only as male flowers, and perfect flowers which produce functional pollinia as well as a functional stigma. The two types of flowers are different morphologically but a transition can be found between them. I have observed the same situation in *M. buccinator* Lindl., from central Ecuador. Certain plants were noted which produced the same large flowered type with little contortion of the column and a very large stigmatic surface which Allen noted in *M. lineatum*. On other occasions the same plants produced smaller flowers with strongly contorted columns and reduced stigmas.

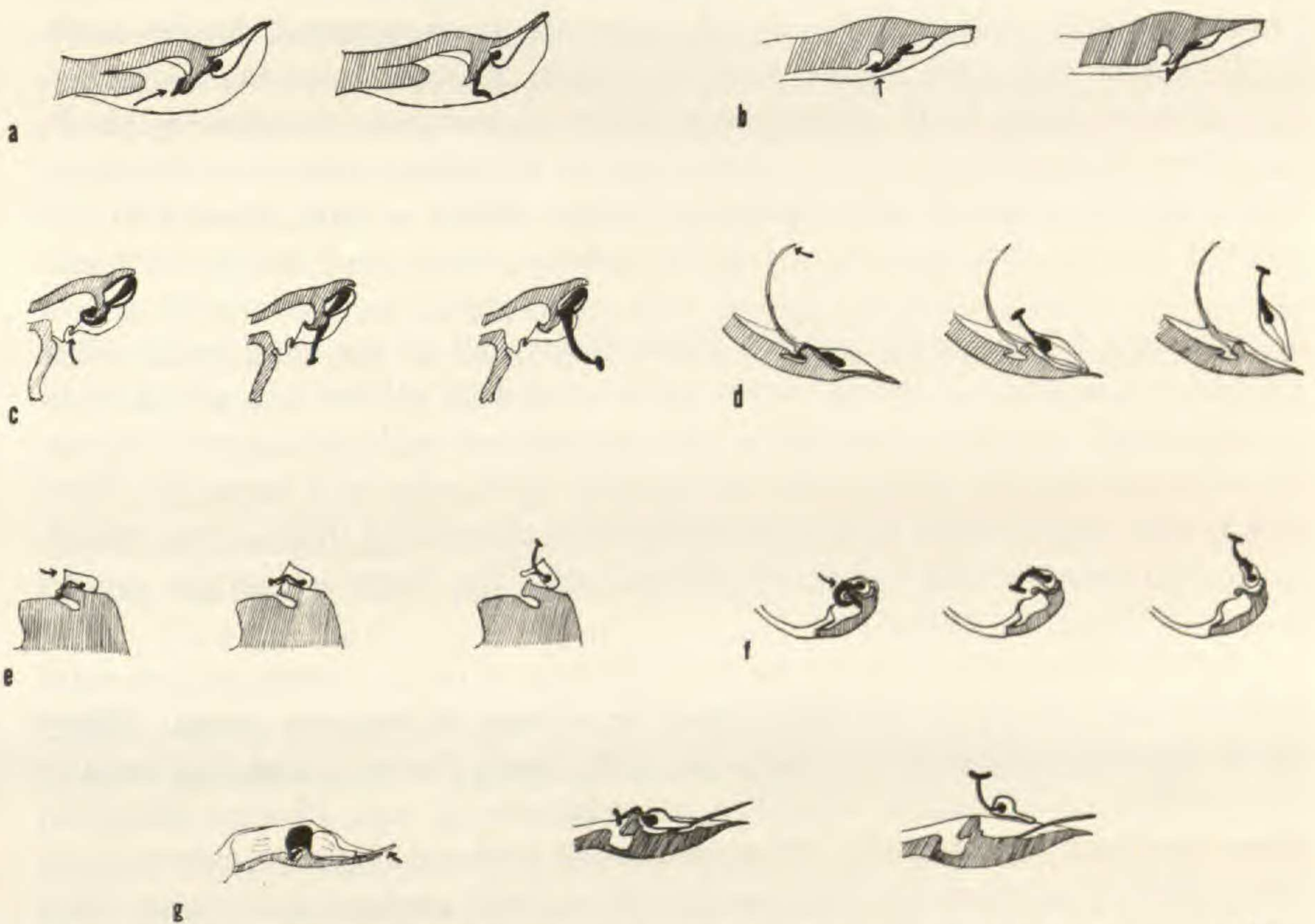


Figure 1. Action of the pollinaria discharging apparatus in the various groups within the *Catasetinae*. The arrow indicates the point of contact which releases the stipe. a. *Catasetum thylaciochilum* Lem. b. *Catasetum russellianum* Hook. (Slightly exaggerated). c. *Catasetum discolor* Lindl. d. *Catasetum platyglossum* Schltr. e. *Catasetum* aff. *suave* A. & S. f. *Cycnoches ventricosum* Batem. g. *Mormodes buccinator* Lindl.

Figure 2 shows two views of a flower of *M. colossus*, the first taken with the anther in place and the second taken 24 hours after removal of the anther. The column has straightened and reorganized itself so as to function as a female flower. This phenomenon has not yet been observed in other species of *Mormodes*.

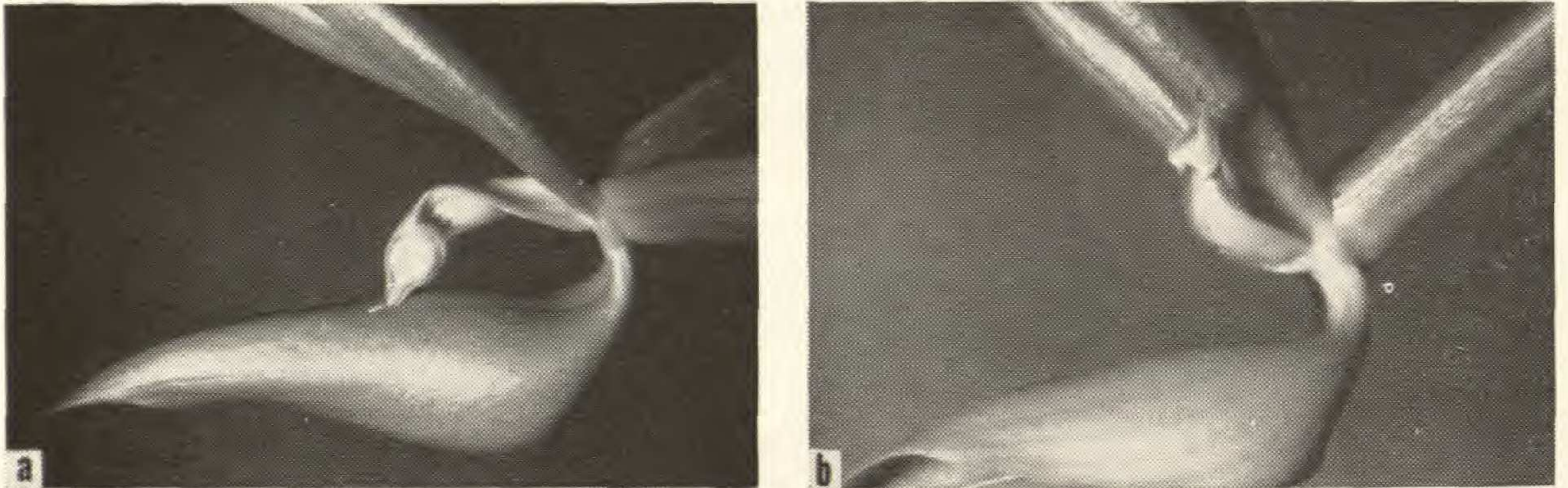


Figure 2. Twisting of the colum in *Mormodes colossus* Rchb. f. a. Flower with the anther in place. b. The same flower 24 hours after removal of the pollinarium.

The factors which make it possible for a plant of this group to produce male flowers during one season, female flowers in the following season and perhaps a mixed inflorescence in the succeeding season have never been clearly explained. There has been considerable speculation about temperature relations triggering one type or the other. Also an intrinsic ability on the part of the plant to decide whether it should produce one sex or the other has been suggested. Studies made by the author over a 14 month period in coastal Ecuador involving *Catasetum macroglossum* Rchb. f., *C. platyglossum* Schltr., *Cynoches lehmannii* Rchb. f., and *Mormodes buccinator* Lindl., indicate that the production of male versus female flowers depends primarily upon ecological factors. When a plant growing in full sunlight has adequate moisture during the growing season and has its roots embedded in a suitable substrate (rotting wood is apparently most favorable) it will be robust and will generally produce female flowers. If on the other hand, either sunlight or humidity is lacking, or the plant is growing on the bark of relatively smooth-barked tree, it will normally not be as robust and will produce male flowers. The substrate does not appear to be as important as the other two factors for plants with female inflorescences have occasionally been observed on living trees, though in all such cases the trees had deeply fissured bark. The factor of sunlight appears to be particularly important.

Experiments conducted at the Instituto Botánico of the University of Guayaquil indicated that the sex of the flower could be changed during one season. Thirty robust plants of *Catasetum macroglossum* with female flowers which had been in full sunlight under natural conditions were brought in and 15 were placed in dense shade and 15 in full sun. These plants had produced their first inflorescences before the full development of the pseudobulb and still retained their leaves. New inflorescences were produced and all plants in shade flowered male. Thirteen plants placed in full sun continued to produce female inflorescences. Two plants which were not quite as robust as others produced inflorescences with both male and female flowers present. Large plants which had produced male inflorescences in

the early part of the season produced female inflorescences when placed in full sun for the remainder of the season.

It seems clear from these experiments that determination of sex depends largely upon growing conditions of the individual plant. Robust plants growing in full sun usually produce female inflorescences. The chemical differences in the plants which are producing one sex as opposed to plants producing the other have not been investigated. There is the possibility that the production of female flowers may be due to carbohydrate balance or, on the other hand, it may also be due to a hormone balance which is affected by sunlight. A similar situation has been reported in *Cannabis sativa* in which the production of male or female flowers was controlled by presence or absence of hormones.

As a general rule very few plants in a population are growing under conditions conducive to the production of female flowers. In the *Catasetum macroglossum* populations growing in the tropical deciduous forests of coastal Ecuador, approximately 21 male inflorescences for each female inflorescence were counted. In populations growing in the regions of greater humidity which are now planted to cacao and coffee, the trees provide considerable shade and the count was 46 male inflorescences to one female. In populations of *Cynoches lehmannii* growing in old cacao plantations around Quevedo the count was 27 male inflorescences to one female. No accurate results were obtained in the population of *Mormodes buccinator* due to the shortage of specimens, however it was noted that the only two plants which produced the female type inflorescences were growing in full sun in ant nests and had extremely large and robust pseudobulbs. Seven other plants were found growing in partial shade which did not have large pseudobulbs and all produced male inflorescences.

The discrepancy in numbers between the male and female inflorescences produced is apparently important in the ecology of the plants. As a rule the male flowers in all species are short lived, lasting at most four or five days. Their segments are usually thin in substance and wilt within hours after the pollinaria have been discharged. Within two or three days after opening their fragrance becomes strong and they wilt shortly thereafter. If the pollinator does not discharge the pollinarium within a day or two after the fragrance becomes strong they are often discharged automatically or by the slightest movement of the wind. The female flowers, on the contrary, are very long lasting, occasionally persisting up to six weeks. They are usually large and of very heavy, fleshy substance and do not emit their fragrance until seven or eight days after they have opened. It would seem logical that more male flowers would be needed since insect visitation is often rather haphazard and it would be highly important to the fertilization of the female flowers to have a large quantity of short-lived, fragrant male flowers in the vicinity. With a succession of numerous short-lived male flowers available to the pollinators the possibilities of the pollinator having pollinaria attached when he visits the female flower would be greater.

POLLINATION

Pollination within the subtribe Catasetinae is very poorly documented and the accounts which have been published are inaccurate in many points. We have

observed pollination in *Catasetum macroglossum*, *C. platyglossum*, *C. suave*, *Cyanoches lehmannii*, *C. egertonianum* and *Mormodes buccinator* (Dodson & Frymire 1961b). Allen (1952) has reported the pollination of *Cyanoches ventricosum*, *Catasetum oerstedii* and *Mormodes histrio*. Hoehne (1933) reported on *Catasetum cernuum*. Östlund (unpublished) very accurately recorded the pollination of *Mormodes histrio*, *M. uncia* and *M. lineatum*. Unfortunately, these species represent a very small portion of the actual number of species in the subtribe but they do represent both subgenera in *Catasetum* and *Cyanoches*, and four species of *Mormodes*. A discussion of pollination in each of the species which we observed should establish the basic patterns of pollination involved.

It would appear that all species in the *Catasetinae* are pollinated by bees of the family *Apidae*, subfamily *Euglossini*. Two genera important in pollination of the *Catasetinae* are *Eulaema* and *Euglossa*. We have not observed any other visitors to the flowers. For a more extensive discussion of these bees and their habits see Dodson (1962).

Pollination of *Catasetum suave* (this name is tentatively used until the identity of earlier names can be definitely fixed) was observed in June of 1960 at a site 12 kilometers east of Balzapamba on the road to Guaranda in the Province of Bolívar. This locality is on the western slope of the Andes at an elevation of 1400 meters. The plants are terrestrial and grow on the faces of road cuts. Pollination is effected by males of *Eulaema cingulata* (L.). The bees approach the flowers, which are carried on racemes of 10-20 flowers each, and land upon the open surface of a flower attempting to reach the source of the strong clove oil-like fragrance which emanates from the cavity of the lip (fig. 3). The flowers are nonresupinate, therefore the lip is uppermost in the flower. In attempting to thrust its head into the cavity of the lip, the bee moves the small hump on the anther cap and the stipe is released, flinging the sticky viscidium upwards where it strikes the bee either on the trochanters of his legs or in front of the first pair of legs. The stipe of the pollinarium, immediately after attachment to the bee, is curled and does not dry and straighten out for several minutes. This tends to insure that the bee will have flown on to another plant and will effect cross-pollination. The viscidium covers the stigmatic surface of the flower so that the pollinarium must be removed before pollination can occur. When a bee with pollinarium attached comes to a flower and repeats the attempt to enter, the pollinia are guided into the stigmatic cavity, trapped in the narrow extremities of the cavity, and pulled from the bee upon his exit from the flower.

Lankester (1960) reports the pollination of the other species from this group, which he (possibly quite correctly) called *C. dilectum*. The flowers of this species are essentially similar to *C. suave*. The primary differences between the two species lie in the sub-capitate inflorescence, strongly reflexed tepals, smaller flowers and enlarged callus of *C. dilectum*. According to Lankester *C. dilectum* is pollinated by a species of *Euglossa*. His description indicates that the activity of the bees is similar to what I observed in the pollination of *C. suave*.



Figure 3. *Eulaema cingulata* (Fab.) visiting the flowers of *Catasetum* aff. *suave* A. & S.

Catasetum russellianum is representative of the closed flowered types of the subgenus *Clowesia* and experiments with living male bees of *Eulaema cingulata* at the Missouri Botanical Garden indicate that this species of *Catasetum* with its only slightly sensitive anther uses a different mechanical system for attaching the pollinarium. The bee, in attempting to reach the saccate portion of the lip, near the base of the column, touches the stipe of the pollinarium and the viscidium is released and swings down into such a position that in withdrawing from the flower the bee will push against the viscidium with its metathorax. Upon subsequent entrance and exit from another flower—allowing time for the anther cap to dry and fall—the pollinia are left behind in the narrow stigmatic cavity.

The subgenus *Catasetum* has a rather different system of pollination primarily because there are two sexes of flower involved. Two species from this section were observed and have essentially the same system although the flower form is different. Two or three days after opening, the mature hood shaped male flowers of *C. macroglossum* begin emitting a strong musky odor. Male bees of four species of *Eulaema* were observed visiting the flowers. These were *E. cingulata* (L), *E. tropica* (L), *E. bomboides* Friese and *E. speciosa* Moc. The bees grasp the labellum, which in this species of *Catasetum* is uppermost in the flower, and enter upside down (Fig. 4). After entry they do not extend their tongues, but scratch the inner surface of the labellum with their fore legs using the same action as a dog digging a hole. At the same time their antennae brush over the scratched surface. Chemoreceptive pads on the tarsi of the bees (which are present in all male bees of the Euglossini) apparently allow the bee to taste the liquid which is emitted from the scratched surface of the labellum. While scratching at the inner surface of the saccate

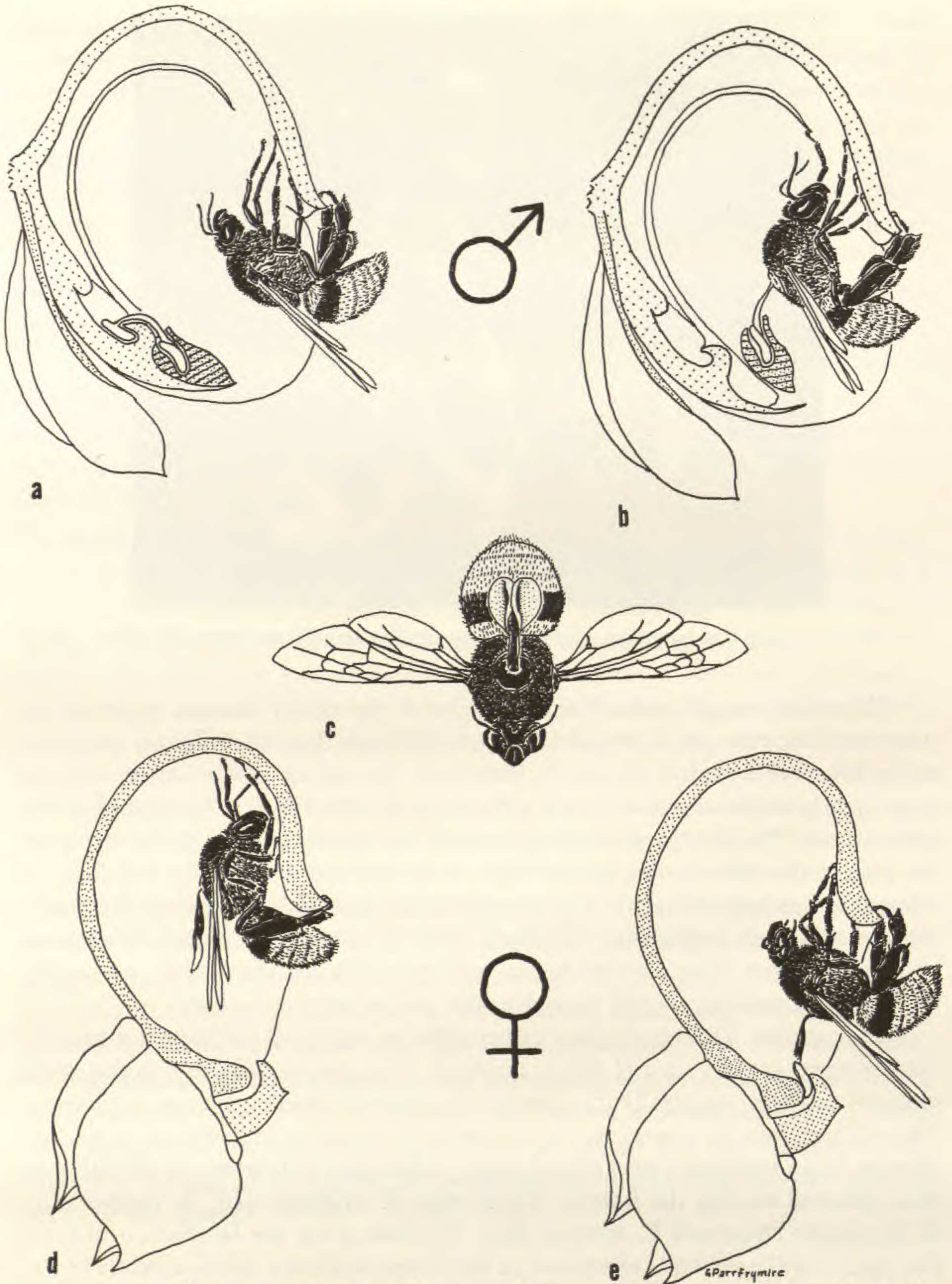


Figure 4. Illustration of the pollination of *Catasetum macroglossum* Rchb. f. by *Eulaema cingulata* (Fab.). a. Male bee entering the male flower. b. The bee scratching at the surface of the lip and touching the antenna which fires the pollinaria out toward the pollinator with the viscidium striking the thorax of the bee. c. Bee in flight with the pollinarium attached to its thorax after the anther cap has fallen. d. Same bee entering the female flower and scratching the surface. e. Bee preparing to leave the flower. Note the pollinia being guided into the stigmatic pocket of the column where they are removed by leverage as the bee struggles free.

labellum the bee contacts one of the antennae which are extensions of the sides of the rostellum and hold the anther cap and stipe of the pollinarium under tension. The tips of the antennae are located just over the deepest point of the saccate labellum where the strongest odor is emitted. The movement of the antennae triggers the release of the pollinarium. The pollinarium is propelled upward and outward, the sticky surface of the viscidium foremost, and is stuck to the thorax of the bee. The adhesive substance of the viscidium sets rapidly, and the stipe hinges back at the point of attachment to the viscidium lying flat along the dorsal mid-line of the abdomen of the bee. The bee may then proceed in its wandering to a mature, aromatic, female flower.

The female flower takes somewhat longer to mature than does the male and begins to give off a strong odor on the third or fourth day after opening. The non-resupinate female flowers last up to a month if not pollinated and continue to emit their strong fragrance during the day; however, the fragrance disappears within hours after pollination, and the stigma swells shut. Bees are attracted to and enter the female flowers much as they do in the male flowers. When a bee with a pollinarium attached to its thorax enters a flower, the stipe, hinging at the viscidium, swings down in line with the stigmatic cleft. As the bee backs out to leave the flower, one or both of the pollen masses are guided down on the back side of the lip and are caught in the stigmatic cleft. They are then wrenched free—by leverage—from the weak bonds with the stipe and are left to fertilize the flower.

Pollination in *C. platyglossum* is essentially identical, the only major difference being that the male flowers are resupinate with the open lip lowermost in the flower (Fig. 5). The bee simply lands on the open labellum, walks to the basal cavity and touches the antennae, setting off the same process as in *C. macroglossum*. The female flowers are so nearly identical to *C. macroglossum* that it is not possible to separate the two species from the female flower alone.

Hoehne (1933) has reported on the pollination of *Catasetum cernuum* (Lindl) Rchb. f., in Brazil, by *Euglossa violacea*. *Catasetum cernuum* is similar in many respects to *C. platyglossum*, having male flowers which are open rather than hooded as in *C. macroglossum* and its allies. The flowers of *C. cernuum* are considerably smaller than those of *C. platyglossum* and are highly colored with orange and red

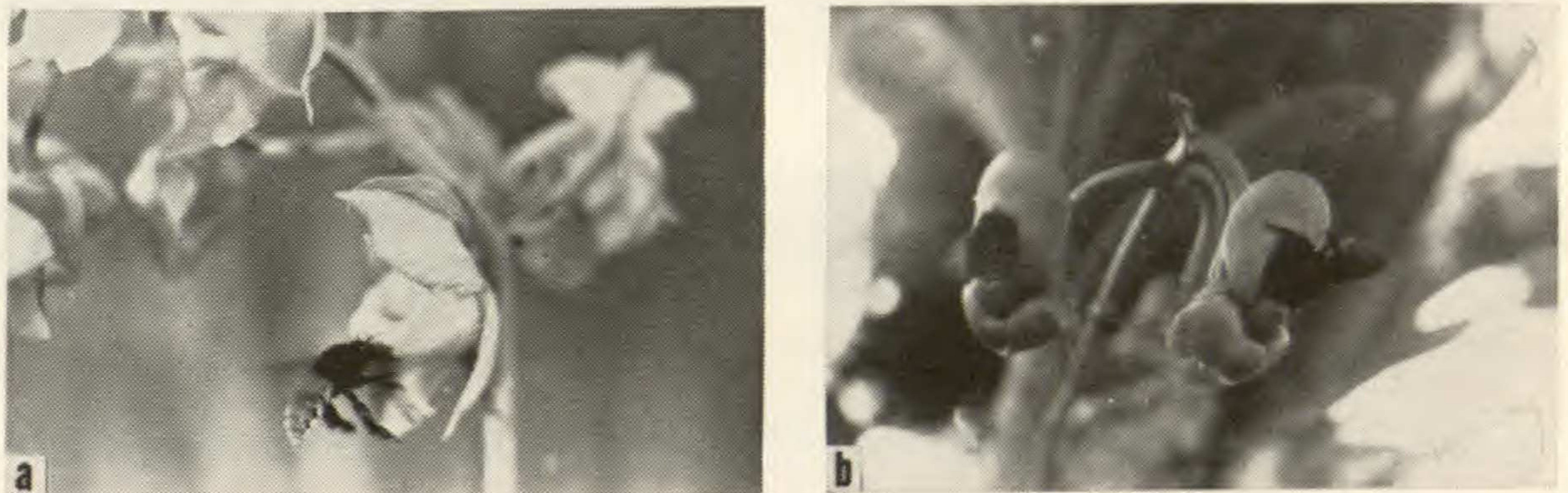


Figure 5. a. Male *Eulaema tropica* (L.) visiting the male flowers of *Catasetum* aff. *platyglossum* Schltr. b. Male *Eulaema cingulata* (Fab.) visiting the female flowers of *Catasetum platyglossum* Schltr.

spots. This species is representative of a large number of species from South America which have open male flowers and more or less fimbriate lips. Hoehne's description indicates that the pollination process is essentially the same in this species as in *C. platyglossum* with the exception that *C. cernuum* utilizes bees of the genus *Euglossa* as pollinators. Probably most of the species in the group allied to *C. cernuum* are pollinated by *Euglossas*.

The pollination process in *Cycnoches lehmannii* appears very complex but in reality is quite simple. The system depends on perfect placement of the bee in relation to the lip and sexual apparatus of the flower. In order to place the bee properly the flower has developed a lip which is nonresupinate, forcing the bee to land in an inverted position, with the source of the odor located at the apex of the callus of the lip. The female flowers appear to have an odor that is a little stronger

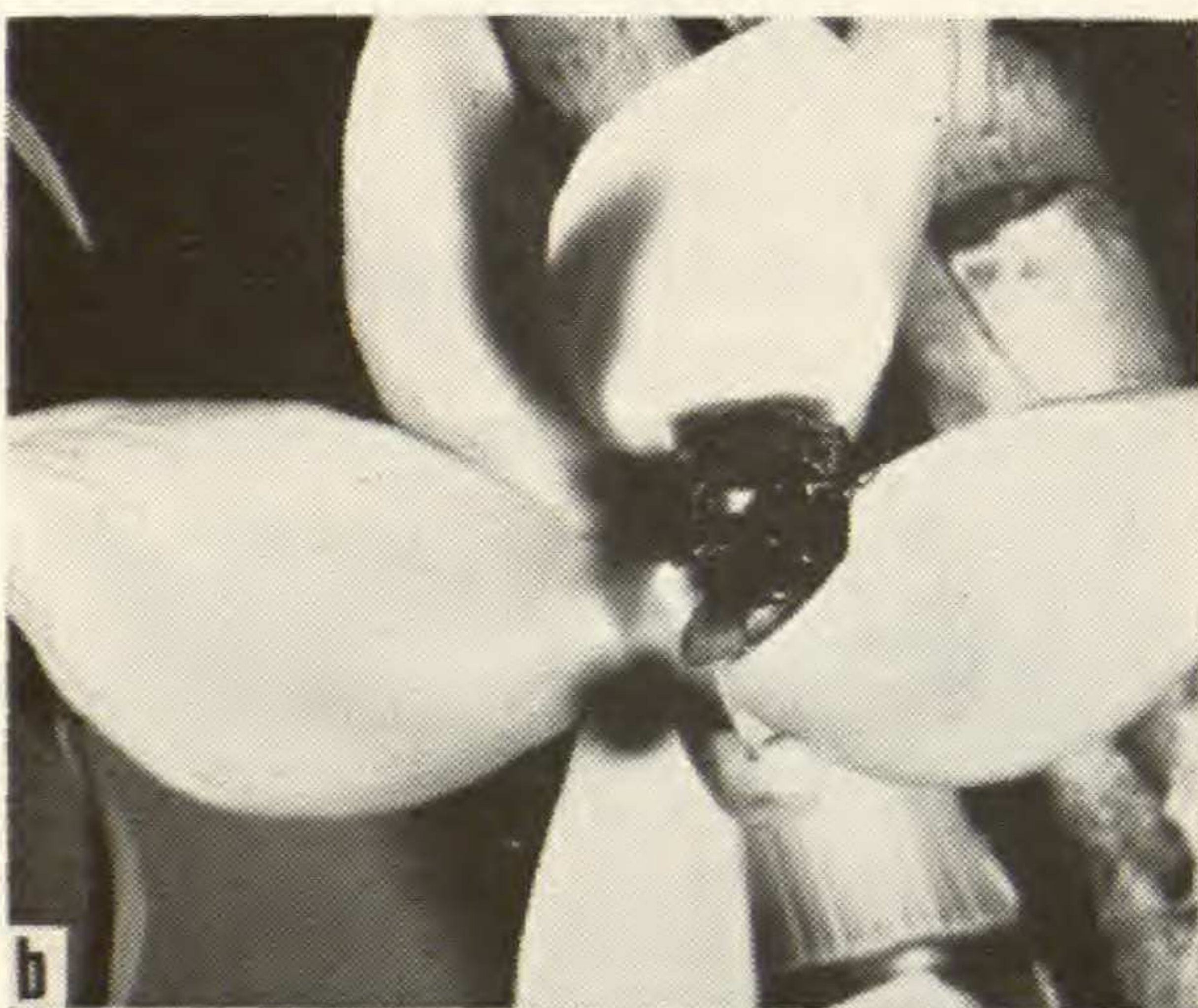


Figure 6. Male *Eulaema cingulata* (Fab.) pollinating *Cycnoches lehmannii* Lindl. a. The bee has touched the apex of the anther cap with its abdomen causing the pollinarium to be discharged and the viscidium to be attached to the apex of the abdomen. b. Male bee scratching at the apex of the callus of the lip of the female flower. c. Bee falling from the callus of the female flower (note the pollinarium extended from the abdomen of the bee which will be caught by the hooks of the apex of the column).

and more penetrating than the male flowers. The male bee of *Eulaema cingulata* approaches the male flower and lands on the inverted lip, gradually swinging around into an inverted position with the 2nd and 3rd pair of legs grasping the edges of the lip. (Fig 6). The first pair of legs are brushed back and forth on the apex of the callus. The odor appears to emanate from between the apex of the callus and the lip. The extended callus of the male flower forces the bee—in attempting to get closer to the source of the odor—to swing his abdomen down and release his lower pair of legs. This is an extremely awkward position for the bee and the lower portion of the abdomen of the bee brushes the trigger mechanism of the column. The brushing of the tip of the anther cap releases the viscidium which is held under tension in what would normally be the stigmatic region in a bisexual flower. The stipe whips the viscidium around striking the bee on the last sternum of the abdomen where it sticks by means of its rapid drying cement. The anther cap remains over the pollinia and the stipe is curled around the tip of the bee's abdomen. The stipe of the pollinarium, through differential drying of the two surfaces, gradually straightens out and after about 40 minutes has straightened to a stiff pendant position. The anther cap remains in place covering the pollinia for about two to three hours before drying sufficiently to fall off. The pollinarium is then ready for the bee to pollinate the female flower.

The female flower is constructed differently. The position of the column and stigma is quite different from the male flower in relation to the callus, being much shorter and thicker. The callus is not as extended as in the male flower and the bee has little difficulty in hanging and scratching on the callus tip. When the bee is ready to fly he must fall for a short distance to be able to revert to a flying position. In falling, the bee, through his predetermined position on the callus is oriented in such a manner that in passing the column the pollinia are caught by the finger-like processes of that structure. One of the pollinia is caught and is stripped from the stipe. Within a few hours the stigma swells, closing around the pollinia, the odor ceases, and the flower parts wither; the pod ripens about a year after pollination.

Pollination of *Cycnoches egertonianum* Batem. was observed in the Amazon drainage area of the southeast Ecuador. *Cycnoches egertonianum* is a member of the heteromorphic group of *Cycnoches* in which the male flowers—unlike the group to which *C. lehmannii* belongs—are strikingly different from the female flowers. The male flowers of this species are small and are carried on long pendant racemes. The lip is somewhat different from that of *C. lehmannii* in that the claw is thin and flexible and the blade is divided into numerous fleshy terete divisions. Male bees of *Euglossa viridissima* were observed pollinating this species. (Fig. 7). The bees would land on the blade of the lip which would then swing down with the weight of the bee. This action caused the tip of the bee's abdomen to touch and lift the anther cap on the apex of the column, discharging the pollinarium which became affixed to the bee much as in *Cycnoches lehmannii*. The female flowers are nearly identical to those of *C. lehmannii* except that they are somewhat smaller and are darker green in color. The pollination of the female flower is essentially the same as discussed in *C. lehmannii* above.

Pollination of *Mormodes* has been reported for four species (Allen 1952 and Östlund unpublished). We observed bees with pollinia attached to their thorax visiting the female flowers of *M. aff. buccinator* in Ecuador. The bees, *Euglossa viridissima*, landed on the outstretched lip and proceeded to scratch the surface of the lip with their front pair of feet. (Fig. 8). In moving around on the lip the pollinaria on their backs came in contact with the very broad stigmatic surface and the pollinia became detached. Though the anther of the pistillate flower in *Mormodes* can eject the pollinarium, it is held up and far away from the lip of the flower in a position which would be very difficult for a bee to encounter and discharge. In the male flowers the column is twisted in such a way that the apex of the column lies in contact with the lip. Usually the twisting places the back of the column in contact with the lip and the anther, located on the ventral surface, is facing outward. A small terete finger or tubercle formed from the tip of the column is in contact with the tip of the anther cap. This tubercle lies on the surface of the lip and the slightest movement moves the anther cap allowing the viscidium to be released. The viscidium, carried by the stipe, springs around and strikes any object which has moved the tubercle. The cement on the viscidium quickly dries leaving the pollinarium attached to the insect. After about 30 minutes have passed the stipe

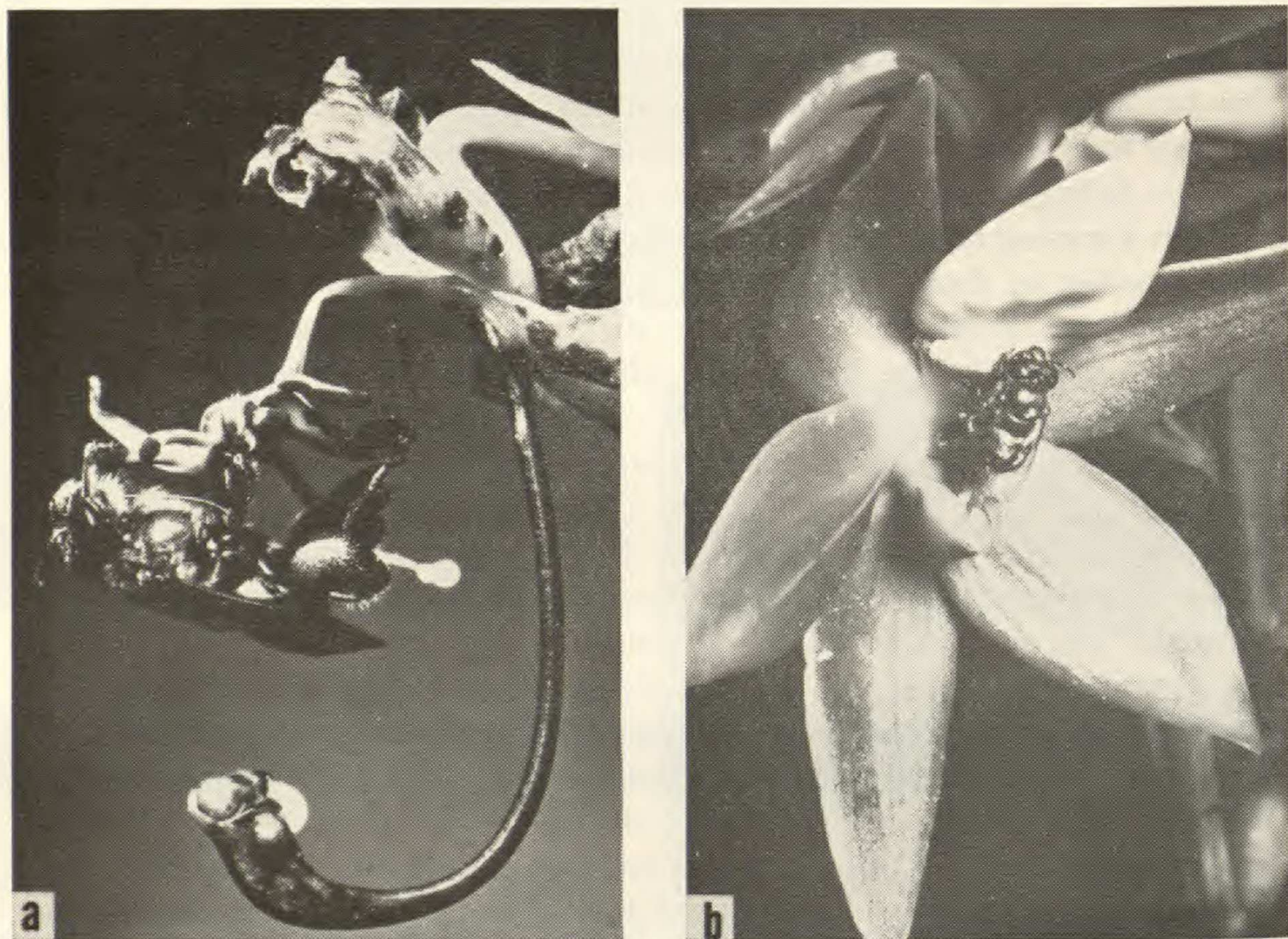


Figure 7. Male *Euglossa viridissima* Fr. pollinating *Cycnoches egertonianum* Batem. a. Male bee hanging from the flexible lip of the male flower (note the pollinarium extending from the apex of the abdomen of the bee). b. Male bee scratching at the callus of the lip of the female flower (note the pollinarium which has been deposited in the stigma).

straightens and the pollinia are held erect from the thorax of the bee in such a position that when the bee walks under the stigma of a flower, contact is made.

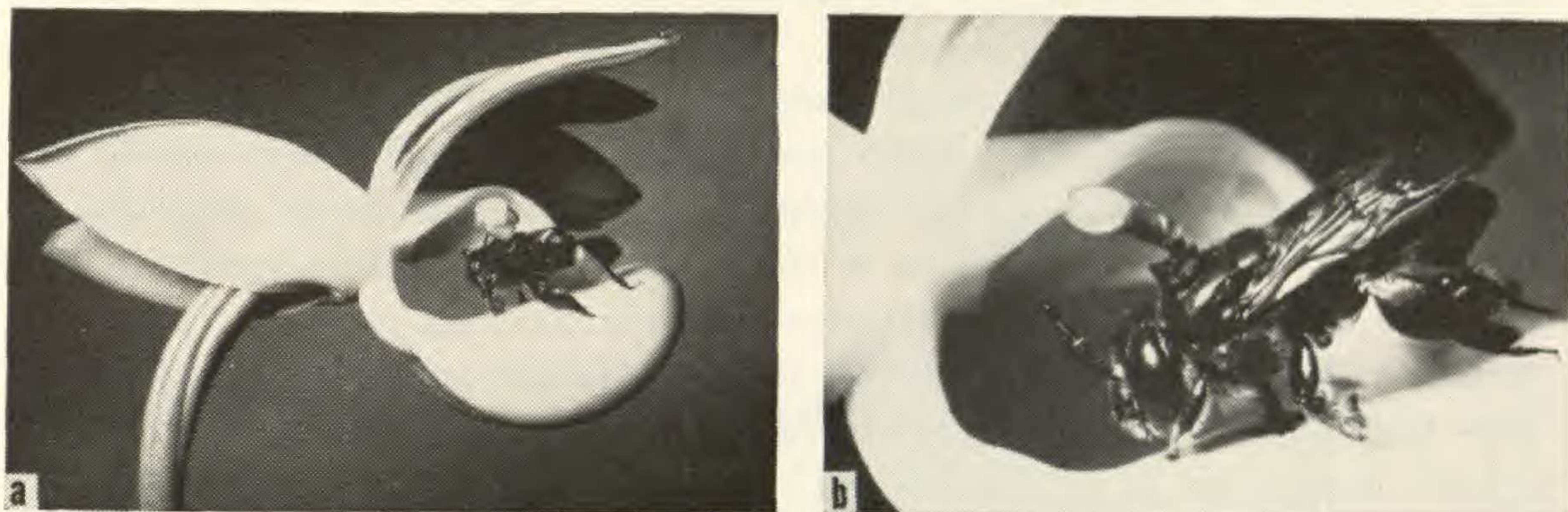


Figure 8. Male *Euglossa viridissima* Fr. pollinating the flower of *Mormodes buccinator* Lindl. a. Bee walking around on the lip of the flower immediately after discharging the pollinarium which can be seen curled up and attached to the thorax of the bee. b. The same bee at a later time showing the pollinarium attached to the thorax of the bee. (Note that the stipe of the pollinarium has straightened placing the pollinia in position to be deposited on the stigma in the background.)

In no instance of pollination observed by me, in any of the above mentioned species of the Catasetinae, did the bees gnaw on the lips of the flowers as reported by Darwin (1877), Crüger (1865), Porsch (1955), Allen (1952 & 1959) and as so eloquently described by Ames in *Catasetum* (1945). The bees were never noted by us to even touch the surface of the labellum with their mandibles and they did not extend their tongues. It is possible that chewing or gnawing do actually occur during pollination of these orchid species in Panama or Trinidad but this hardly seems reasonable since the same species of bees are involved as in Ecuador. Östlund (unpublished) reports the same phenomenon of scratching in the pollination of *Mormodes lineatum* in Mexico. He also pointed out that the bees did not gnaw the flowers.

We have noted numerous small bees and wasps which do gnaw the flowers of these and other orchids but which are too tiny to actually effect pollination. None of the Catasetinae provide nectar or has nectaries. The bees, apparently in all cases, scratch the surface of the lip at the point of origin of the odor and then touch the liquid released, with the sensory pads on their feet. This liquid appears to have an intoxicating effect on the bees because they cease to be wary and then can be approached without being frightened. The bees often spend considerable time at one plant and will enter the same flower repeatedly. On each occasion, they enter, scratch the surface of the lip for about 60 seconds, leave the flower and hover for about 40-60 seconds, apparently checking for danger, and then reenter the flower. After the bees have been visiting a particular flower for some time, it can even be removed and the bee will continue to search out that flower from the odor.

Perhaps the most significant factor brought out by these observations is the fact that in both *Catasetum* and *Cycnoches*, species groups have become both morphologically and ecologically distinct by their adaptation to different kinds of pollinators. Of even greater interest is the fact that the two kinds of pollinators are

closely related, have similar habits and similar morphology. Their principal differences are in size and response to different fragrances produced by the flowers for their attraction. Indications are that the bees have been on the scene for a much greater period of time than the orchids. The orchids have been able to utilize the two types of bees as a crutch, so to speak, in speciation. The opportunity of using different kinds of pollinators, which would not overlap and thereby would not nullify the adaptation to distinct mechanical systems, may be as important in speciation to a group of this nature as are the development of incompatibility and genetic barriers to crossing in many other groups of flowering plants. Speciation in these orchids could occur by adaptation to one pollinator and later to another and then back again. Such speciation would, of necessity, be on a large scale with drastic changes in morphology of the flowers expected. Elimination of intermediates by early extinction would leave large discontinuity between groups and would present to the systematist clear-cut groups even at the generic level. The development of such strikingly different morphological features as found in the *Catasetinae* and the *Stanhopeinae* (Dodson and Frymire 1961a) may be attributable to just this sort of speciation.

VARIATION IN POPULATIONS

Population variation in the subtribe *Catasetinae* has long been a problem in species classification. The problems in this group are not so great on the generic level. For the most part the genera are amply distinct, but the delineation of species has been unusually difficult. Taxonomists working with preserved material have been plagued by this problem and the all too common solution has been to describe each troublesome specimen as a new species, based upon the obvious floral differences from any other known species. Unfortunately, though this has been the easiest method for handling the problem, it has not reflected species differences. Until recently no studies have been attempted on extensive living populations in their natural habitats.

The problem of extreme population variability is not peculiar to the *Catasetinae*. It is also quite evident in certain species of nearly all genera of the *Stanhopeinae*, the *Maxillariinae* and in many genera of the *Oncidiinae* and *Epidendrinae*. The only usable taxonomic treatments of large variable groups in the orchids have been done recently by Paul Allen in *Cycnoches* (1952) and *Chysis* (1955). His treatments of these two troublesome genera reflect his deep knowledge of the extent of population variation gained by personal knowledge of the taxa involved. His reduction of a series of 50 named species of *Cycnoches* to 7 with 4 subspecies demonstrates, for the first time in the group, not only the excessive number of named variants but also phylogenetic trends within the group. As an example, he reduced 14 named species to one, *Cycnoches egertonianum* and retained three subspecies which represent geographical and population trends.

Similar work is needed in the genera *Catasetum* and *Mormodes*. Many names have been applied to individual variants from variable populations of *Catasetum*, particularly in South America where population studies have been nonexistent and few preserved specimens are available in herbaria. In many cases names have been applied to plants without any knowledge of their origin.

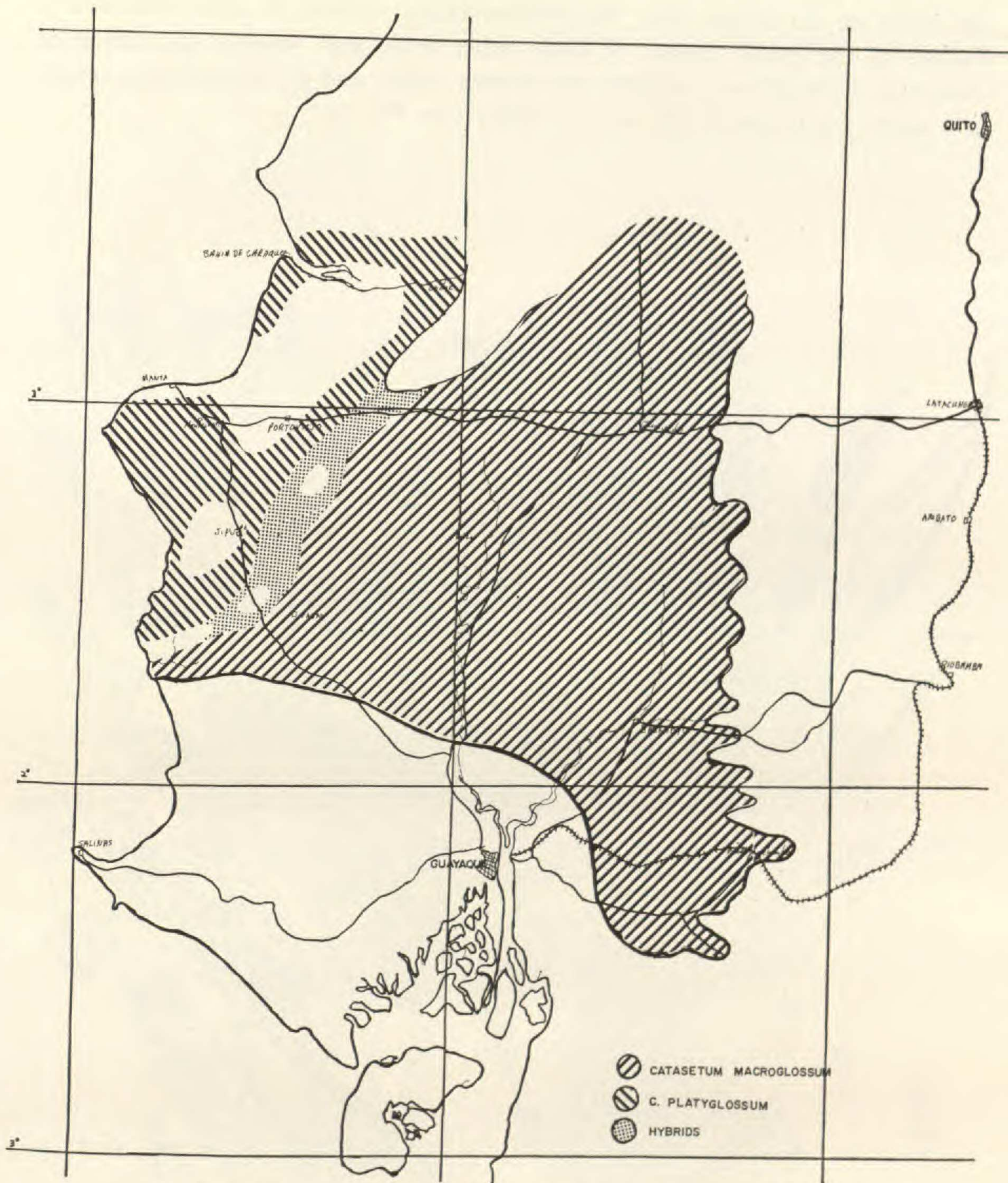


Figure 9. Map of western Ecuador showing the distribution of *Catasetum macroglossum* Rchb. f., *C. platyglossum* Schltr. and their hybrids.

In coastal Ecuador, populations of two highly confused species of *Catasetum* are found in quantity. These are *C. macroglossum* and *C. platyglossum*. During the early months of 1958, 1960, and 1962 I had the opportunity to observe and study hundreds of flowering plants of these species and some rather startling observations were made. The two species were apparently once separated by a range of mountains, the Cerros de Colonche, which run north and south through the coastal plain paralleling the Andes. These mountains effectively split the coastal plain into two valleys with the eastern valley about 50 miles wide and flanked by

the Andes on the eastern side. The western valley is about 30 miles wide and is flanked by the Pacific Ocean. A large rather dense and variable population of *Catasetum macroglossum* occupies the eastern valley and *C. platyglossum* occurs in a sparse population in the western valley (see Fig. 9).



Figure 10. *Catasetum macroglossum* Rchb. f. showing two inflorescences, the female to the left and the male to the right.



Figure 11. *Catasetum platyglossum* Schltr. showing the male inflorescence.

Until recently [probably less than 200 years as established by comparison of the grazing areas of livestock during the colonial period (1600-1700) and the map in Wolf's *Geografía y Geología del Ecuador* (1892)] the Cerros de Colonche with its rainforest-clad slopes provided an effective barrier to gene exchange. A drying trend throughout the coast, caused by an apparent shift in the Humboldt current, has reduced the width of the rainforest, particularly in the passes between the higher areas. In these passes the two species have come together and the result has been the production of a series of hybrid swarms of bewildering variation.

Figure 10 shows a plant with male and female inflorescences of what could be considered as typical *C. macroglossum*. Figure 11 represents a plant with a male inflorescence of typical *C. platyglossum*. The female flowers of both are so nearly identical that no statistical difference could be noted between the two. Figure 12 shows a series of specimens taken from a representative group at Las Peñas, a pueblo some 30 kilometers south of Jipi-japa in the province of Manabí on the western slopes of the Cerros de Colonche. All specimens were collected within a radius of 50 meters. Several of these individuals could easily be given specific names and in fact a plant very similar to number 4 of figure 12 which I collected from this same locality was donated to the Los Angeles County Arboretum where it was seen by Fowlie (1962) who suggested very strongly that it be named as a new species since it did not fit any of the descriptions contained in Mansfeld's monograph of the genus.

The problem became doubly significant when it was discovered that the same bees visit and pollinate all the various types of flowers indiscriminately, regardless of their color or form. Bees of *Eulaema tropica* were observed passing from the flowers of the plant illustrated as number 4 of figure 12 to number 8 of the same figure. One bee visited a flower of number 4 and received pollinia on its thorax and then visited number 8. Another bee visited the same flower of number 4 and did not receive pollinia from that flower since it had already been triggered. He then flew to number 8 and did receive pollinia from a flower on that inflorescence. Both bees could then presumably fly to female flowers of either type and effect pollination. This behavior on the part of the bees is apparently the reason for the variation noted where populations of the two species come in contact. The importance however, is that variation is apparently permitted by a lack of selection for a particular type of flower since visits by bees were frequent for all types of flowers and no particular preferences were noted.

These species have evolved morphologically and physiologically to withstand a wide range of ecological habitats, from the xerophytic conditions of the coastal thorn forests to the wet tropical cloud-forests on the slopes of the Andes. Though having diverged in the past to form separate populations with very characteristic floral structures, the genus has maintained integrity of interfertility within all of its taxonomically definable species. Regardless of extremes in other floral structures, that part of the male flower critical in ensuring cross-fertilization, the column and its incumbent ejectable pollinarium, show remarkably little variation. Any consistent deviation from the condition that allows the successful ejection of the

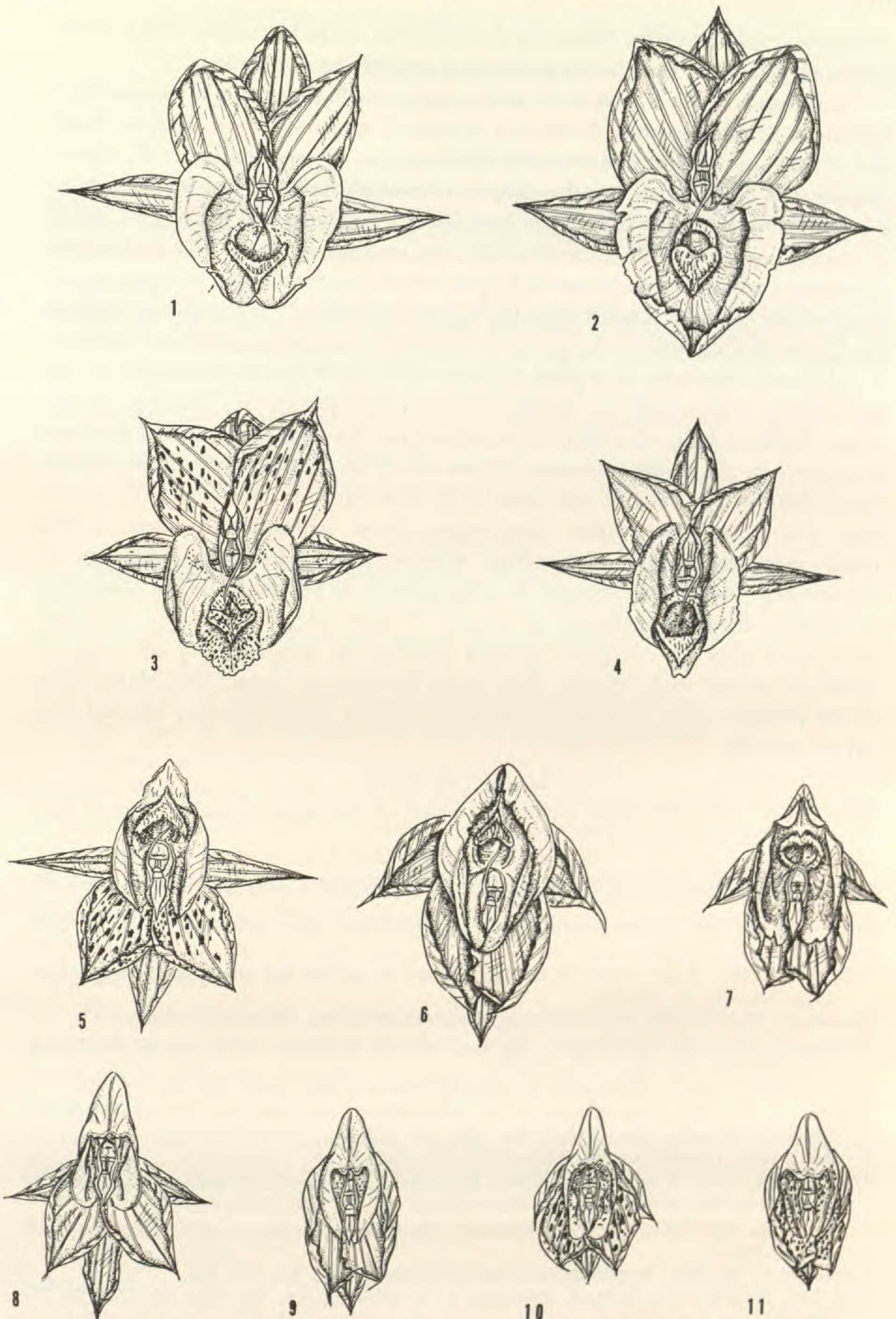


Figure 12. A series of flowers, taken from a population at Las Piñas, Ecuador, demonstrating the extremes from a hybrid swarm between *Catasetum macroglossum* Rchb. f. and *C. platyglossum* Schltr.

pollinarium and its precise deposition on the thorax of the bee would tend to eliminate that plant as a contributor to the gene pool of the population.

A situation which is apparently quite comparable to these populations and their hybrids in Ecuador occurs in Venezuela between *C. macrocarpum* A. Rich ex Kunth and *C. pileatum* Rchb. f. *Catasetum macrocarpum* is very similar to *C. macroglossum* and *C. pileatum* is quite close to *C. platyglossum*. A vast series of intermediates between these two concepts have been encountered and many were named by early taxonomists before the situation was understood. Plate 502 in *Lindenia* illustrates a series of these presumed hybrids which is quite similar to a comparable series which could be selected from the *C. macroglossum*-*C. platyglossum* series in the Cerros de Colonche.

Although *Mormodes* as a genus is amply distinct, the species boundaries or concepts within it are nearly nonexistent. Several recent papers, i.e., Teuscher (1954), Allen (1959) and Correll (1941) have pointed out the confusion involved but have done little to clarify the situation. There are three distinct kinds of *Mormodes*; those with strongly 3-lobed lips, those with obcordate lips and those with cordate lips. The factor which makes classification almost impossible, however, is that nearly every conceivable intermediate between these three basic types can be encountered. Not a great amount of information is as yet available but there may be definite, distinct populations of certain of these intermediate types. In other cases, there may be extremely variable populations demonstrating all types of variations on the three themes. This group promises to present formidable taxonomic problems, and there is the possibility that a simple clearcut account will not be possible.

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